

ON THE PHYLOGENY OF SOME DIPTERA BRACHYCERA.

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(Two Text-figures.)

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The section of Diptera referred to here has long been known as the Brachycera division of the suborder Orthorrhapha, but Dr. R. J. Tillyard (1926, p. 345) has reversed the status of these two names making Brachycera a suborder that incorporated all Diptera except the Nematocera and the term Orthorrhapha becomes the name of the division.

The relationship between the various families is deduced from the researches of various authors. The families are fast becoming better understood so it is possible to illustrate their supposed affinities diagrammatically and to discuss them from this aspect. J. R. Malloch (1917, pp. 173-181) dealt with the larval and pupal characters of these families and he formed six superfamilies which are now reduced by Tillyard to three as instanced by the table given below. The simplicity brought about by this reduction has much to commend it.

Family.	Superfamily name used by:	
	Malloch.	Tillyard.
LEPTIDAE TABANIDAE	TABANOIDEA	TABANOIDEA
STRATIOMYIIDAE (Some non-Australian families)		
NEMESTRINIDAE CYRTIDAE		
SCENOPINIDAE THEREVIDAE	THEREVOIDEA	
ASILIDAE APIOCERIDAE MYDAIDAE BOMBYLIIDAE		
EMPIDIDAE DOLICHOPODIDAE	EMPIDOIDEA	EMPIDOIDEA

A diagram of the relationships between these families is very readily formed and it is the purpose of this paper to point out some of the more striking features arising from this method of allying the families, to indicate some of the weaker points and to incorporate some of the lines along which my own researches are tending to show a development regarding the superfamily Asiloidea.

The genealogical tree given below contains three main branches, the first of these is the superfamily Tabanoidea into which come all forms containing a pulvilliform empodium, and it is further divided into three divisions, the Tabanid-Leptid stem, the Stratiomyiid stem and the Cyrtid-Nemestrinid stem.

The first two of these contains insects that are largely associated with water, many breeding in marshes and such-like places, but the third, the Cyrtid-Nemestrinid stem is not associated in this manner. It is of interest to note that the land-breeding family Nemestrinidae contains species that have a wing-venation in which there is a marked tendency for the apex of the veins to move towards the costa and this is repeated in the other entirely land-breeding section the Asiloidea. In the light of our present knowledge this must be regarded as parallel development but possibly it has a deeper significance, for the position of the Cyrtid-Nemestrinid stem within the superfamily Tabanoidea appears to be somewhat anomalous, differing so markedly as it does in many structures. It has apparently parasitic habits throughout the entire group, though possibly some cases may prove to be an advanced type of predatory habits, differing in this respect from the other Tabanoidea.

The Tabanidae and Leptidae have amongst their numbers what may be regarded as the nearest to the primitive venation for this particular superfamily, but in antennal structures they are considerably advanced and specialized, the nearest to the primitive type being perhaps that of the genus *Petecorrhynchus*.

The Stratiomyiidae, on the other hand, have a very specialized venation as the radial vein has moved bodily forward towards the costa, which specialization must not be confused with that of the Nemestrinidae and of the Asiloidea where only the apical parts of the veins have so moved forward. The most advanced type in the Stratiomyiidae is to be found in the genus *Ophiodesma* (Kertész, 1923, p. 118 under the name *Diapontomyia*) where not only has the radial moved forward but also the median, this vein becoming fused with the radial, the radial-median crossvein being obliterated in the process. In antennal structures there are many forms that must be regarded as approaching the ten-segmented primitive type, and many forms have also preserved the primitive elongate abdomen, where each, or most, of the segments are as long as, or longer than, wide.

The primitive interradiar crossvein seems to have become atrophied in the Tabanid-Leptid stem, missing in the Stratiomyiid stem and preserved in the Nemestrinid-Cyrtid stem; it occurs in the genera *Cyclopsidea*, *Trichopsidea* and *Exeretoneura*, the last of these has also retained a strong trace of the primitive ten-segmented antennae and moreover it is the only form known to me that indicates the possibility of its stem having arisen from a type with an elongate abdomen.

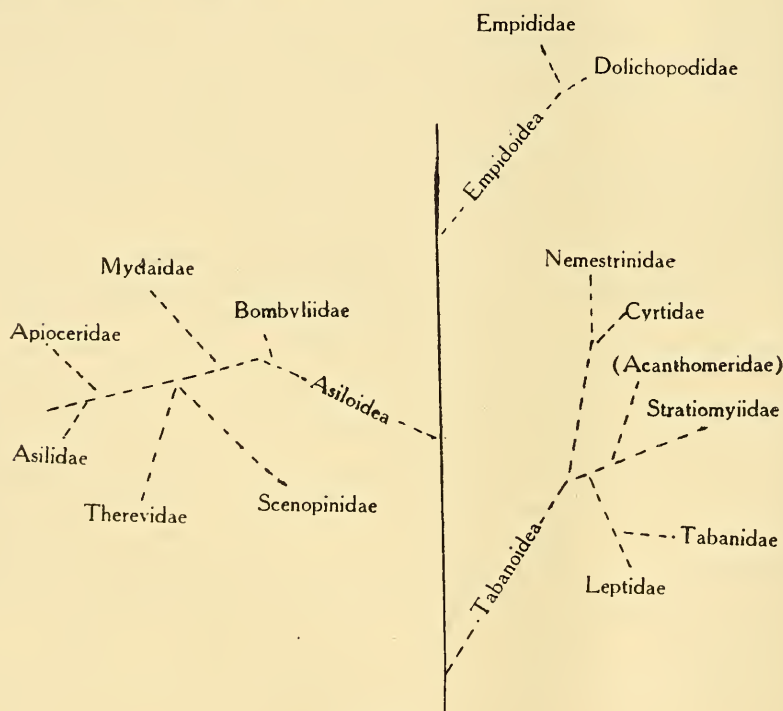
The second superfamily, the Asiloidea, contains insects that do not have a pulvilliform empodium and apparently have evolved from a somewhat advanced land-breeding type. This hypothetical type differs from that of the Tabanoidea by having only seven distinct antennal segments, a larger number has not been found represented in any existing genus and indeed the occurrence or the traces of this seven segmented antennae is persistently represented throughout the

superfamily. The small family Scenopinidae is said to be allied to the Therevidae owing to the similarity it bears to that family in the larval stages, but the relationship is very anomalous.

There are two main branches in this superfamily, the Bombyliid stem and the Asilid stem. The first of these seems to have lost entirely one of the branches of the median vein but in other respects there is a marked parallel development to that of the Asilid-stem.

In the Bombyliidae the first radial vein often becomes short, running to the wing margin much nearer to the base than is usual and this has allowed the other branches of the radial to run to the costal margin when they have curved upwards as is found to be the case in so many genera. The median vein also shows a tendency to curve upwards as M_1 runs into R_2 in certain cases.

In the Asilid stem, the first radial remains normal and when the following veins are strongly curved upwards they run into this vein and not to the costal



Text-fig. 1.

margin. This is a parallel development to that of the Bombyliidae resulting in a strikingly distinct vein pattern.

All the Mydidae and Apiceridae, and practically all the Therevidae (the exceptions may not belong to this family) are provided on the female with genital spines that are similar in every respect to those of certain groups of the Asilidae, and which are not found in the Bombyliidae or families other than the Asiloidea.

The third superfamily, Empidoidea, is composed of two families, the Empididae and Dolichopodidae, both of which contain flies that have larvae associated with water as is the case with the Tabanoidea, but besides being without the pulvilliform

empodium they are also marked by the restriction of the cubital and anal veins, these being considerably reduced in length.

The diagram (Text-fig. 1) of the relationship so far discussed would conform, I believe, to something near the average diagram that would be drawn by any entomologist who had a fairly comprehensive knowledge of the Brachycera, and to the work so far accomplished in building up the relationships between the various families. Differences of opinion would centre chiefly about the position of the Nemestrinid-Cyrtid stem and of the family Scenopinidae, and also concerning the exact relationships of the Asiloidea families, excluding the Bombyliidae.

There can be little doubt that the spines at the apex of the female abdomen, spines used for raking the ground when oviposition takes place, are significant in so far as all those insects that contain them must be considered as derived from a common stock and that they do not occur outside the Asiloidea suggests that they originated within the Asiloidea itself probably remote from the deviation of the Bombyliid stem which itself has an analogous row of genital bristles that are used in quite a different manner.

I have stated above that the Asiloidea were derived from a stock having but seven antennal segments and this is probably correct in the main in so far as the other segments had largely amalgamated with one or other of these seven. It is possible that the whole ten may have been indicated by annulations, etc., and in building up the structure from the lowest type of antenna in the Asiloidea I have yet found, that of the Mydidae, I would unhesitatingly place the first two segments as 1 and 2, the shaft following as 3 and 4 (these are clearly enough indicated), the apical flattened sections as 5, 6, 7 and 8, the minute process at the extreme apex, situated on the edge just within a depression as 9, and finally the minute spine on this minute process as 10. These last two are so easily overlooked, the 5-8 so completely amalgamated that there thus becomes only five of the original ten segments clearly defined but nevertheless seven are indicated. The abdomen of the Mydidae is quite primitive but modified in its type and the vestige of the interrarial is present, but in every other respect the wings have a very specialized venation. The head is deeply excavated between the eyes very much as it is on most of the Asilidae. There are plenty of hairs above the oral opening but they do not form the appearance of the typical moustache of the Asilidae as they are soft and slender.

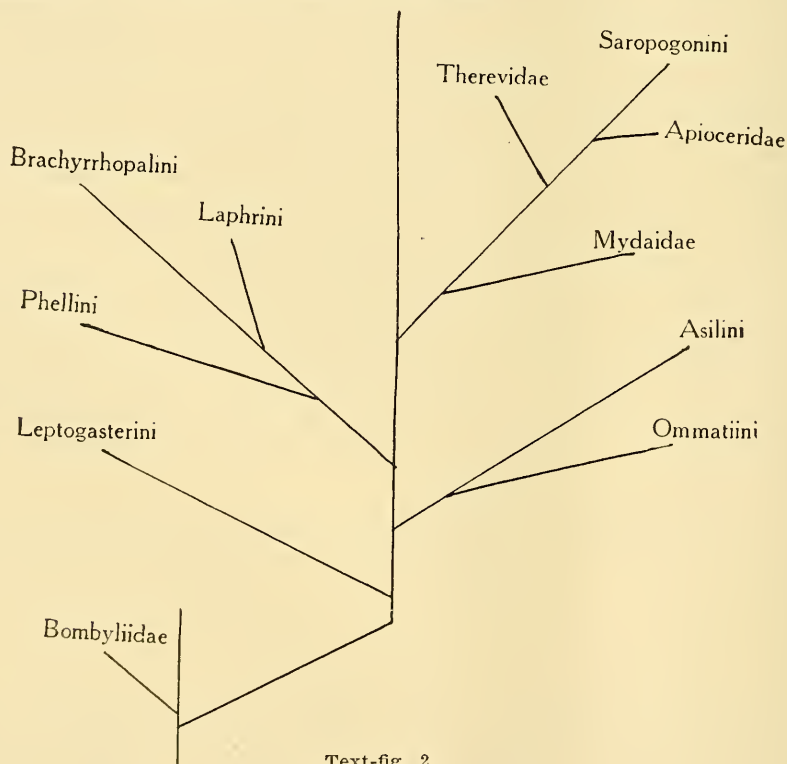
The Apioceridae have only four antennal segments clearly defined, the last being a short and strong spine. The head is slightly excavated between the eyes as on certain Asilidae, the abdomen is much shortened, and the antennae are situated too near the oral opening to permit of a moustache being formed there; the hairs on the very small area so formed are soft and slender. It is evident that the Apioceridae are very advanced along their line of development, the venation being specialized and the interrarial crossvein is entirely missing.

The Therevidae consists of a number of genera of diverse forms and amongst their numbers are to be discovered many primitive forms, one specimen that has a rather long abdomen also has five antennal segments, all easily detected, the last being a spine, and in addition there is the rudiment (or possibly remnant) of an Asilid-like moustache; the hairs along the oral margin consisting of a series of bristles such as is found on certain Asilidae but more slender, comparable with that of *Neocyrtopogon*. In no case has there been discovered any form with the head that is to be compared with the excavated head of the Asilidae and Mydidae. With regard to venation, this is fairly simple but invariably lacks

the interrarial crossvein; at most M_4 runs into M_3 whilst the cubital and anal veins may also meet near the apex. The genus *Clesthena* is excluded from these remarks and given special consideration below.

As already pointed out, all the three families, Mydidae, Apioceridae and Therevidae are provided with spines at the apex of the female abdomen. This character occurs in many Asilidae and in view of the similarity of other characters already referred to, characters that unite these four families, it seems probable that these genital spines indicate a common origin for all those forms containing them.

If it were possible to separate the family Asilidae into two or more sections, one stem of which has arisen from a stock containing these spines, the remainder from a stock that did not develop them, then it would be reasonable to suppose that the Mydidae, Apioceridae and Therevidae had a common origin with one stem of the Asilidae, which in the present case would be the tribe Saropogonini, a section of the Asilidae, not the whole stock. It does not seem reasonable to suppose that the spines could have developed independently and assumed identical formations as is to be found in the four families.



Text-fig. 2.

The genus *Clesthena* was originally placed in the Leptidae by White, but subsequently removed by me to the Therevidae; I now believe the position here to be anomalous. It is certainly one of the Asiloidea and shows a marked advance from the primitive stock. Five antennal segments are discernible, the abdomen is rather short and conical, the venation lacks the interrarial crossvein and M_4 runs

into M_3 , otherwise the veins are simple. It may be an off-shoot of a more primitive Asilid type rather than that of the Therevid stem and if so the genus should prove of exceptional interest. Similarly the American genus *Pherocera* Cole, which is said to be without the genital spines, would also need to be placed elsewhere.

Doubtless these views will be modified by further research, but if they are adopted for a working hypothesis, it will be necessary to amend the portion of the genealogical tree relating to the Asiloidea as in Text-fig. 2.

In concluding these remarks I would draw attention to the apex of the female abdomen which, in the Tabanoidea, is provided with simple cerci in all its three stems whilst, in the Asiloidea, these cerci have not been found or perhaps are modified in certain cases such as to provide the lamellae on the female ovipositor of the *Asilini*. It is possible other characters of the female genitalia have yet to be found that would be suggestive in regard to these relationships and so a study of this aspect should yield some important data.

To the list of works referred to in this paper, there are also added others that bear upon the subject dealt with and amongst these will be found diagrams that will serve to illustrate the remarks made above.

Postscript, added 13th September, 1927.

Whilst the above paper was going through the press, a Bombyliid of the genus *Comptosia* was found using the bristles at the apex of the abdomen in the manner identical to that exhibited by the *Saropogonini* when ovipositing. The genitalia of this Bombyliid were thereupon studied in considerable detail and the conclusions drawn were to the effect that the type of ovipositor exhibited by it approached nearer than any other examined to the hypothetical type from which the *Saropogonini* and Therevidae were derived. Moreover this hypothetical type which can now be defined with some assurance, may have been the origin of all the widely varying types found in the Asiloidea, for certain features of the *Asilini* type are to be traced to it through the genus *Neoaratus* and the spines of the ovipositor on the genus *Philonicus* may yet be shown to have had the same origin as those on the *Saropogonini*.

For the immediate purposes of this paper it is necessary to draw attention to the order in which the relationships of the various families and tribes have been built up. This was done on the understanding that the primitive type of ovipositor was represented only by a pair of valves generally greatly reduced, and the end segments of the abdomen were more or less telescopic as in Mecoptera (Tillyard, 1926, p. 340). If this be the case, then somehow in the Asiloidea at least, a modification must have arisen resulting in the building up from a simple to the complex ovipositor that in many cases became permanently exserted. It now becomes advisable to revise this view and perhaps a better conception of the phylogeny within the Asiloidea may be gained by completely reversing the order of the Asilid stem so as to bring the Mydaid-Saropogon branch to the foot where other characters would ally it, and by placing the *Leptogasterini* at the top.

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